Complexity, Predictability and Promiscuity in Human Sexual Preferences

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A thesis submitted in partial fulfilment of the requirements of the University of Lincoln for the degree of Masters of Science by Research, supervised by Dr. Daniel Pincheira-Donoso

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Contributions

This thesis consists of my primary research, which is to be examined as part fulfilment of my Masters by Research degree. Below presents a summary of the contributions made to this research.

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This is the primary research of my Masters by Research degree, of which I have completed all stages and thus, this is my own research work.

Study design: **LPH**, DPD; *Questionnaire design:* **LPH**, DPD; *Data collection*: **LPH**; *Data analysis and interpretation*: **LPH**; *wrote manuscript*: **LPH**; *project supervision*: DPD.

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ABSTRACT

Reproductive success (fitness) is the currency for species evolution, and therefore, the establishment of sexual relationships is one of the most fundamental interactions underlying life on Earth. Sexual selection theory aims to explain the strength and implications of sexual bonds as a result of traits that evolve to influence sexual encounters and thus, reproductive success. Humans offer a valuable 'model' to understand the nature of sexual behaviour, especially because their preferences can be directly communicated by individual participants, in contrast with non-human animals in which preferences are inferred from behavioural observations. The high social complexity of humans has led to multiple approaches to understand individuals' attitudes and behaviours within an eco-evolutionary context, particularly with regards to investigating how 'attractiveness' traits influence sexual relationships, and how the expression of these traits matches sexual outcomes (i.e., as a proxy for mating success). Although humans traditionally fall between a polygyny and serial monogamy mating system, it remains poorly known how promiscuity is associated with a ubiquitous factor underlying human social/sexual dynamics: 'love'. This research investigated how promiscuity (measured as numbers of self-reported sexual partners and as the desire to be promiscuous) and simultaneous love (individuals declaring whether they can 'fall in love' with more than one person simultaneously) are affected by a number of different traits (gender, age, self-assessed attractiveness, sexual orientation) and interpreted under predictions of sexual selection theory. Using a newly generated dataset, it was quantified how self-assessed attractiveness traits influence the expression of promiscuous desires across participants. The majority (84.5%) of participants displayed a desire for promiscuity. Gender and sexual orientation are the main variables in which there is a relationship in participant's desires for promiscuity and simultaneous love. Notably, this research revealed that more than half of the individuals in the sample (57.1%) expressed the possibility to love more than one person simultaneously. This finding goes against fundamental norms underlying monogamous sexual relationships in most human societies. Collectively, this thesis provides novel data to further discuss promiscuity in humans.

INTRODUCTION

A central prediction of sexual selection theory states that the intensity of competition over sexual partners depends on mating systems and the expression of secondary sexual traits (Darwin, 1871; Andersson, 1994). One fundamental example of this is the long-standing observation that as the numbers of females decline relative to the numbers of males, the intensity of competition for access to sexually mature females increases, thus increasing pressures to promote the evolution of male phenotypes which enhance the chances of gaining matings (Darwin, 1871; Andersson, 1994; Bell, 2012). Therefore, the intensity and direction of sexual selection on phenotypes strongly depends on the social and mating environment, which can promote the adaptive evolution of different mating strategies (Andersson, 1994; Shuster & Wade, 2003).

Mating systems are classified based on common patterns of mating interactions, largely dictated by the commitments of males and females to parental investment in their progeny (Trivers, 1972; Shuster & Wade, 2003). Therefore, the evolution of sexual behaviours and traits are commonly explained following traditional Bateman's principles influenced by a combination of interacting factors, such as sex ratios (Kokko & Jennions, 2008), sex differences in parental investment (Trivers, 1972), and sexual conflict over fitness-related strategies (Parker, 2006; Brown *et al.*, 2009). Mating systems are also constrained by ecological pressures and resource availability (Emlen & Oring, 1977), and thus, ecological factors play fundamentally decisive roles on sexual interactions via the expression of sexually attractive phenotypes that depend on high degrees of energy allocation (Andersson, 1994; Cornwallis & Uller, 2010; Nosil, 2012). The sex which invests more heavily in offspring is the choosier and the limiting resource for the other sex (i.e., the source of selection). Therefore, the less-invested sex competes more strongly over access to mates, leading to increases in the intensity of sexual selection on the individuals' traits competing over access to matings (Trivers, 1972; Clutton-Brock & Parker, 1992; Andersson, 1994). These interactions, and the predominant role of females as the source of sexual selection stem from fundamental reproductive differences between the sexes, notably the fact that most males produce thousands of gametes daily, while the gamete stock of females is considerably more limited (Andersson, 1994; Bell, 2012; Pincheira-Donoso & Hunt, 2015). Therefore, the predominant tendency is for males to be the less committed sex, both in choosiness of sexual mate, and

level of parental care provided to subsequent offspring. This translates into the idea that males are prone to indiscriminate multiple-mating (polygyny), while females are expected to be choosier in selecting their mates to secure better quality fathers for their offspring (Tregenza, 2003; Arnqvist & Rowe, 2005).

In most vertebrates, polygyny is widespread (Clutton-Brock, 1989; Reynolds, 1996). In polygynous mammals specifically, females are generally constrained by gestation and obligate parental care, thereby males tend to experience higher intensity of sexual selection, yet are freer to gain greater fitness benefits from multiple mating (Harcourt *et al.*, 1981; Shuster & Wade, 2003). However, increasing research exploring the adaptive benefits of polyandry (reviewed in Yasui, 1998; Jennions & Petrie, 2000; Slatyer, *et al.,* 2012) concur it is also frequently beneficial for females to mate with multiple males (Hrdy, 2006; Borgerhoff Mulder, 2009; Brown *et al.*, 2009). Theoretically, by mating with more than one male of high quality, females can increase their fitness through direct male-provided resources and indirectly via the acquisition of 'good genes' and genetic diversity for and among offspring (Yasui, 1998; Jennions & Petrie, 2000; Tregenza & Wedell, 2002), thereby maximising likelihood of offspring survival and reproductive success. In other words, choosiness among multiple mates provides a pool of high quality partners that offer, at the same time, good genes and high genetic variation for the progeny (Yasui, 1998; Tregenza & Wedell, 2000). However, despite such potential benefits, many studies also question how these benefits trade-off with many costs of polyandry (Slatyer, *et al*., 2012). For example, given the often damaging nature of sexual interactions that lead to sexual conflict, the costly act of sexual reproduction is heightened when females engage in multiple matings. In fact, meta-analyses of mating rates suggest that females repeatedly engaging in mating, experience longevity costs from the 'benefits' of higher fertility, from ensuring sufficient sperm supply and higher offspring survival (Scharf, *et* al., 2015). However, many of the arguments for the genetic benefits of polyandry are controversial, due to lack of direct genetic evidence for improved offspring performance (Slatyer, *et al.,* 2012). Given this highly contentious nature of polyandry, there is active debate, highlighting the complexities of promiscuity in relation with differing mating systems (Yasui, 1998; Tregenza & Wedell, 2000). Therefore, it is clear that the evolution of sexual interactions and mating systems is not straight-forward.

The evolution of mating systems and sexual interactions has gained a central place in evolutionary biology (e.g., Andersson, 1994; Shuster & Wade, 2003; Bell, 2012), and is an

exceedingly popular research topic when considering humans (Miller, 2011). Men and women are "extraordinarily different" social and sexual units (Symons, 1980), not only from the viewpoint of responses to selection as a function of anisogamy (i.e., reproduction via dissimilar gametes), but also possess distinct sex-specific mate preferences and reproductive strategies that also heightens the sexual conflict (Buss & Schmitt, 1993; Arnqvist & Rowe, 2005). Research on human mating systems has examined how mating preferences have been shaped throughout evolutionary history, by investigating the behaviours of 'ancestral-like' human societies (Dixson, 2009; Geary *et al.*, 2011) or by drawing observational comparisons from closely related primate relatives (Harcourt *et al.*, 1981; Harcourt & Stewart, 2007). These retrospective conclusions suggest that approximately 80% of traditional human societies were 'naturally' polygynous. However, this degree of polygyny is often slight given that even the most indiscriminately promiscuous males are limited by their resource capabilities to support the associated needs of maintaining multiple relationships (i.e., even the highest quality males may only have enough resources to support a few females) (Marlowe, 2000), resulting in relatively few sexual partners in comparison to some other species capable of hundreds. However, given the narrow scope of 'historic' evidence (mainly marriage accounts and birth records), quantifying the evolution of human mating interactions can be greatly improved by assessing the spectrum of sexual attitudes and behaviours among contemporary human populations (Low, 1988; Schmitt, 2003). Thus, the generation of large-scale datasets from current populations is an approach used to investigate human sexual preferences and attitudes from an evolutionary perspective.

The emerging availability of such data on sexual behaviours and mating preferences from both Western societies and cross-cultural comparisons reveals that humans engage in mutual choice serial monogamy (i.e., males and females choose exclusive relationships one after another) (Buss & Schmitt, 1993; Schmitt, 2003), often with both sexes engaging in additional extra-pair matings (Emlen & Oring, 1977; Dixson, 2009). On the one hand, theory predicts some men commit to a constrained bi-parental investment into offspring, but may seek to increase their reproductive success through additional matings where possible (Buss, 1988; Buss & Schmitt, 1993). On the other hand, women tend to be more willing to seek an exclusive monogamous relationship. However, it is a more likely tendency for females to only engage in extra-pair matings occasionally with high quality males (Greiling & Buss, 2000; Borgerhoff Mulder, 2009). These sex differences in their mating preferences translate

consistently with high rates (in comparison to that expected in strictly monogamous systems) of extra-pair paternity cross-culturally (Marlowe, 2000; Schmitt, 2003; Scelza, 2011), suggesting male and female promiscuity to be an unequivocal feature of human mating. Interestingly, such evolutionary and behavioural evidence clashes with the perceived preference of strict monogamous relationships, often majorly influenced by society and culture, which drive socially moral standards of sexual interactions (Henrich, *et al.*, 2012). Therefore, in humans, a very special phenomenon expresses with regards to sexual behaviours, in that the intrinsic nature of humans has been shaped by our highly complex social and cultural environment.

Given that a serial monogamous mating system has been shown to be most common in humans cross-culturally (Buss, 1994; Schmitt, 2003; Eastwick *et al.*, 2013; Stewart-Williams & Thomas, 2013), observations suggest this commonality of serial monogamy in humans results from a mixture of favouring 'short term' or 'long term' mating strategies (Simpson & Gangestad, 1991; Penke & Asendorpf, 2008). Mating strategy here refers to individual fluctuations in reproductive behaviours based on mating system. In humans, individuals can incorporate a variety of behaviours from differing mating strategies to succeed in multiple matings that can be both casual and committed relationships (Stewart-Williams & Thomas, 2013). Much of the contemporary literature measures the extent of promiscuous tendencies (i.e., likelihood of extra-pair sexual interactions) using sociosexual orientation (Simpson & Gangestad, 1991; Schmitt, 2005; Jackson & Kirkpatrick, 2007). Sociosexual orientation refers to an individual's preference for seeking 'unrestricted' casual short-term or 'restricted' exclusive long-term relationships, and is extended to assess the willingness of individuals to engage in promiscuous sexual interactions outside a committed relationship (Sociosexual Orientation Inventory) (Penke & Asendorpf, 2008; Lippa, 2009). Recently, Wlodarski *et al.* (2015) suggested that both men and women possess a mixture of *either* restricted or unrestricted tendencies (also termed as sociosexual orientation). This high degree of variation and plasticity within human sexual desires indicates that the story of the human mating system still remains complex, and will probably never completely correspond with one mating classification (Roberts & Havlîcek, 2013).

Evolutionary theory provides the overarching conceptual framework to explain and predict processes shaping the phenotypic nature of species. However, it remains a highly contentious field within social and behavioural research especially in humans, with a variety

of approaches designed for testing the complex behavioural traits described above for our species (Laland & Brown, 2011). Since the mid-1970s, sociobiological debates have emerged regarding the applications of evolutionary theory to human behaviours in the same context as the study of non-human behaviour (Wilson, 1975). When considering why behaviours or desires evolve in animal behaviour, there is an underlying argument that rules such as Morgan's canon should be employed as a guiding principle, which depicts that animal behaviour should be described as simply as possible and without interpretation bias based on human behaviours that are of "higher psychological processes" (Morgan, 1903). Many approaches to investigating human behaviour, prevalent in the fields of human behavioural ecology and evolutionary psychology, draw on the fundamental fact that humans are the product of evolutionary history and shaped by millions of years of selection, resulting in highly complex cognitive and psychological function (Fisher, 2000). Here, this study relied on the view that evolutionary principles will apply to all organisms in different degrees, but that the intrinsic features that define the human species (e.g., their degree of sociality, their natural selection regimes that influence life history adaptations, their exceptional cognitive complexity, among others), make humans a unique case to investigate how promiscuous desires operate under an evolutionary perspective.

One limitation, however, of employing an evolutionary approach to studying mating desires in humans (a cosmopolitan species with high rates of gene exchange) is that evolutionary assumptions have a tendency to over-generalise responses collected form specific individuals into conclusions about humans as a whole species. This may lead to problems especially when data are mostly obtained from specific cultures and societies, thereby ignoring potential cross-cultural differences. Since human cultures vary greatly, as well as an individual's devotion to their culture within social groups, it is important to consider that growing up and living in different cultures has specific impacts on an individual's desires and behaviours, especially when it comes to sexual attraction (as demonstrated in different studies; e.g., see Buss, 1989; Schmitt, 2005). Therefore, cultural impact must be taken into account when collecting data and drawing conclusions. The vast majority of studies within evolutionary psychology most often have data derived from Westernised cultures, based on ease of data collection, and hence this 'geo-cultural bias' makes up a large proportion of our knowledge about the drivers underlying sexual human behaviours (Swami, 2011).

Alongside the impact of culture, society, and gender, sexual orientation is a major measure used throughout the study of human sexual desires and behaviour (Bailey, *et al*., 1994; Little & Mannion, 2006; Phellas, 2012). Sexual orientation is particularly relevant to measure mate preferences, and an important factor to quantify how consistent the predictions of human sexual desires and tendencies known from opposite-sex matings apply to same-sex matings. As expected, a number of studies have shown that patterns of sexual attraction differ depending on sexual orientation (Bailey, *et al.,* 1997; Lippa, 2007; Glassenberg*, et al.,* 2010). Despite these individual differences in tendencies of sexual promiscuity, when comparing the effect of multiple traits on an individual's sociosexuality, sexual orientation has a relatively minor effect compared to factors such as gender. In other words, the tendencies of promiscuous desires across different types of sexualities, e.g. comparing homosexual males and females with heterosexual counterparts, is more likely down to their gender than their sexual orientation (Schäfer, 1977; Schmit, 2007). This study will contribute to a growing interest in the influence of sexual orientation on the evolutionary perspective of human sexual desires, particularly how the drivers of sexual selection influence the desire of promiscuity in individuals who identify as non-heterosexual in comparison to heterosexual individuals.

One fundamental concept, severely overlooked in evolutionary biology, which contributes and importantly influences mating interactions in humans, is love. Ubiquitously considered the greatest emotion across humankind, love features across almost all disciplines (Shaver *et al.*, 1996). There are many complexities involved around the concept of love, which has historically resulted in constant and continuous difficulties faced by scientists or philosophers in creating a universal definition that satisfies all of love (Fehr and Russell, 1991). These complexities are illustrated by Brehm (1985): "*Scientists have had as much trouble defining love as philosophers and poets. We have books on love, theories on love, and research on love. Yet no one has a single, simple definition that is widely accepted by other scientists."* However, despite these intellectual difficulties in defining love, this present study draws on most closely with the definition of love described by Hatfield and Walster (1978), where 'passionate love' is defined as "*a state of intense longing for union with another*." Here, this study simplifies Hatfield and Walster's definition and suggests the expression and intensity of sexual attraction can be derived along an 'attraction landscape' consisting of the interactions between variation in the degree of 'sexual motivation' and 'companionship' (presented in Figure 4). Here, in the case of humans, 'sexual motivation' describes emotions related with

instinctive sexual feelings, e.g. lust, while 'companionship' describes human emotions related with wanting partnership within a relationship even if instinctive sexual feelings are absent.

From a mechanistic point of view, the biological basis of love in humans is a hotly researched topic (Fisher, 2004; Wlodarski & Dunbar, 2014), considered to result from neurochemical reactions in the human adult brain of oxytocin, vasopressin, and sex hormones, governing the stages and intensity of feeling in love (Fisher, 2000, 2004). However, there is difficulty in defining love from an evolutionary perspective, where 'romantic love' is hypothesised to have evolved from the infant-caregiver attachment (Hazan & Shaver, 1987), described as 'unconditional selfishness' (Dawkins, 2006), where a pair-bond attachment evolved as an adaptation for ensuring and maintaining bi-parental care (Quinlan, 2008; Zeifman & Hazan, 2008). In human societies it is thought that maintaining a committed family unit (monogamy) is the most likely to ensure offspring successfully survive until reproductive age (Marlowe, 2000; Finkel & Eastwick, 2015). Thereby, loving individuals are in fact devotedly protecting their reproductive success. However, an evolutionary perspective of love should not be limited to considering that love is restricted to an exclusive monogamous relationship. Instead, to consider how love can also occur in polygamous relationships within humans, promoted by evolutionary drivers. Therefore, another central goal of this study was to expand the concept of promiscuity by adding rather controversial (and socially rejected) phenomena, such as the possibility of "falling in love" with more than one person at the same time – which is an expression of biological promiscuity artificially battled by social/moral principles prevalent in a human society.

Here, this study investigated how the expression of attractiveness traits (factors targeted by sexual selection) influence the desires for promiscuous sexual behaviours in human Westernised societies. Following Bateman's principles and the continuation of more recent predictions within evolutionary psychology (Bailey, *et al.,* 1994; Brown, *et al*., 2009; Lippa, 2009), this study specifically hypothesises that (i) there will be a greater tendency in men to desire promiscuous matings in comparison to women (given the differences in sex and reproductive roles that underlie sexual selection dynamics, as explained above), (ii) there will be a greater tendency in younger people to desire promiscuous matings in comparison to older generations (given the high intensity of selection at peak fertility), (iii) promiscuity tendencies will be higher in those who have higher ratings of self-assessed attractiveness (given more attractive individuals are more likely to succeed in gaining matings), and (iv) individuals who

identify as non-heterosexual are more likely to desire promiscuous mating than heterosexual individuals (given the lower levels of sexual conflict). Additionally, this study hypothesised that love is not only restricted to monogamy, but rather humans are capable of simultaneous love in multiple relationships. This novel measure of love provides novel perspectives to understand the enormous variation in human relationships. Therefore, this study proposes a novel conceptual framework aimed to unify forms of attraction under the metaphor of a landscape based on the two dimensions of sexual motivation and companionship, which describes the positions that different human relationships can occupy on this theoretical space.

METHODS

Questionnaire design

Questionnaires are consistently one of the most popular methodological approaches used across numerous fields of research. This methodology is particularly prevalent throughout research on human sexual behaviours and perspectives (Fisher, *et al*., 2010), given the ease of use for constructing questions that can be widely distributed to reach large variety of participants from across the world using online resources. The use of online questionnaires is ideal for maximum participation, given that people can easily access and complete questions with total anonymity. Therefore, participants are more likely to provide honest, accurate answers, particularly when answering questions on a sensitive topic such as sexual measures. However, this methodology does increase confounding biases, such as over/under estimations of measures of self-assessed attractiveness, which cannot be avoided. After critically assessing a range of suitable of methodological approaches (Fisher, *et al*., 2011; Phellas, 2012; Rea & Parker, 2014), the use of an online questionnaire was decided.

The questionnaire for this study was designed to consider and expand upon SOI-R (Revised Sociosexual Orientation Inventory) (Penke & Asendorpf, 2008), a set of questions designed to measure the individual difference in willingness to engage in casual sexual activity outside of a committed relationship, measured through attitude, desire and self-reported behaviour (Fisher, *et al.,* 2010). Since Alfred Kinsey's pioneering research on questionnaire studies of sexual behaviour (Kinsey, *et al.,* 1948), introducing the concept of sociosexuality, led to development of SOI questionnaires (Simpson and Gangestad, 1991; Penke & Asendorpf, 2008), which have been successfully applied in over 50 publications, despite some

conceptual criticism that SOI has a tendency to simplify measures into a single one dimension, that may not be the most accurate reflection of an individual's sociosexuality (Asendorpf & Penke, 2005; Voracek, 2005). For the purposes of this study, the questions modified from the SOI-R aimed to measure the attitudes and desires of individual's sociosexuality (questions 7, 11, 12, 14, 15, 17, 20), which have shown to be reliable enough to satisfy the outlined hypotheses (Fisher, *et al*., 2011). The response method to the adapted questions in this questionnaire was modified from the original 9-point scale of SOI-R, into a binary 'Yes' or 'No' format for simplicity. Questions 1-6 were demographical and measured factors such as gender, age, sexual orientation etc. (data used as factors in quantitative analyses; see below). Questions 3, 4, 6, 9, 10, 18, 19 were retrospectively excluded from subsequent analyses due to inconsistencies with data collection, such as missing responses to questions or ambiguity in question design. The remaining questions were novel, generated from this research, and aimed to further measure an individual's attitudes towards love in the context of sex and promiscuity (*see Supplementary Material S1 for questionnaire)*.

Data collection

A large dataset of human sexual behaviour and preferences was constructed from the creation of an online questionnaire (described above, *see Supplementary Material S1 for questionnaire*) approved by the College of Science Research Ethics Committee, University of Lincoln (UK). The questionnaire was distributed across several research study websites and social media platforms, 'live' from May – July 2015 (*see Supplementary Material S2 for details*), in order to guarantee as much variation as possible in all measured variables (see details below). The final sample consisted of 713 participants (454 women, 259 men), aged 18-60+, with variation in sexualities (562 heterosexual, 52 homosexual and 99 bisexual(other); *see Supplementary Material S3 for summary of data*). Once the online questionnaire was closed, a case-by-case scan of the entire dataset was performed to check for inconsistences and missing data in order to exclude cases that appeared inaccurate.

Measured variables

The questionnaire consisted of 20 questions (*see Supplementary Material S1*) aimed to provide a comprehensive picture of factors which have previously been linked to human sexual interactions and mating preferences (Buss & Barnes, 1986). First, participants were provided

with a range of basic demographic categories, including age, gender, sexual orientation, number of sexual partners, and self-assessed attractiveness rating. Therefore, these key traits were employed as factors in the subsequent analyses.

To assess the extent of promiscuous desire of sexual interactions, participants answered questions adapted and extended from SOI-R (Penke & Asendorpf, 2008). Participants answered if they desire to engage in a casual sex relationship, whilst in a relationship, or whilst in love with someone else, and their willingness to engage in future casual sexual relationships. In addition, this questionnaire also included novel questions about participant's perception of love. For example, whether they are necessary to one another, or whether they can be separate components of sexual relationships. Subsequently, participants' capabilities to express desire for multiple relationships were further quantified by directly asking whether individuals think it is possible to experience love for more than one person simultaneously. All data were collated and transformed (assigned into numerical categories).

Quantitative analyses

Mating preferences and sexual attraction are known to be influenced by the combination of multiple factors, and to be expressed in multiple ways. Therefore, to test these hypotheses, a Markov Chain Monte Carlo general linear model analysis (MCMC GLMM) (Hadfield, 2010) was performed on the complete dataset. This model tested whether gender, age, sexual orientation, self-assessed attractiveness, and number of sexual partners (as factors) effect the likelihood of multiple dependant variables; the differing responses to desires of promiscuity (Question 17) and attitudes towards simultaneous love (Question 13) (as described above). This approach enables the creation of a single multivariate model that analyses the effects of multiple independent variables on multiple dependent variables, and the interactions between them. Given that the data collected from the online questionnaire (see above) are consistently polynomial (with two or more categories; *see Supplementary Material S3*), and given that expressions of sexual attraction are expected to be driven by multiple factors and often by the interaction of such factors, this is an ideal approach to scan the entire dataset. These analyses also detect whether it is a combination of multiple factors that predict a significant effect on the desire for promiscuity, by accounting for correlations between each variable. These analyses are appropriate in this case for the selected traits which all are predicted to have sizeable

effects on the desire for promiscuity, following sexual selection theory (Shuster & Wade, 2003; Schmitt, 2005; Lippa, 2005).

Prior to running the MCMC GLMM model, the strength of association between each response variable is checked using 'Cramér's association coefficient' approach, implemented using the R package 'RVAideMemoire' (Hervé, 2015), which identified the strength of multiple correlations between each response variable. Given most variables had fairly low but existing correlations (*see Supplementary Material S4*), it can be an accepted use of a multivariate model (MCMC GLMM) to accurately test the effects of multiple factors on these multiple dependant variables. For this model, again demographic information and grouping variables were used as independent categorical factors (age, gender, sexual orientation, self-assessed attractiveness ratings, and number of sexual partners), because these represent highly influential traits in human sexual interactions and mating preferences (Buss & Barnes, 1986) (as described above). Similar to the previous analysis, all relevant responses as the multiple dependant variables were included (*see Supplementary S3/4 for list*). This MCMC GLMM analysis ran simulated combinations of the combined multiple dependant variables with all possible interactions of the independent factors (in this case 100,000 iterations were performed). Once completed, this model tested the significance of each independent factor, and their interactions, on the combined multiple dependant variables. These statistical analyses were performed in R (R Core Team, 2014), using package 'MCMCglmm' (Hadfield, 2010).

Given that the MCMC GLMM model returns an overall outcome for all variables together, once analyses were performed and significant differences between factors were identified, separate univariate analyses of variance (ANOVA) were conducted, in order to identify where significance lies in each grouping variable. In this case, the analysis tests whether significance occurs between additional factors that may influence desires of promiscuity, given that all groups may not be significant but contribute to the overriding result. These statistical analyses were conducted using SPSS Version 22.0 (IBM Corporation, 2013).

RESULTS

Factors influencing promiscuous tendencies

Based on participants' responses, the measures of desire for extra-pair sex (Question 17) and attitudes towards simultaneous love (Question 13) were tested against multiple predictor variables with the following outcomes. First, there is no influence of self-assessed attractiveness on desire for extra-pair sex (Table 1), and simultaneous love (Table 2). Similarly, there is no significant relationship of age influencing desire for extra-pair sex (Table 1) or for belief in simultaneous love (Table 2). Additionally, there is no significant relationship between those participants with a higher self-reported number of sexual encounters influencing the desire for extra-pair sex (Table 1) and acceptance of simultaneous love (Table 2).

Regardless of gender or sexual orientation, the majority of participants (84.5%) were found to express a tendency to desire promiscuity. Overall, men express a higher tendency to desire extra-pair sex than women (Table 1; Figure 1A), and are more likely to believe in simultaneous love (Table 2; Figure 1B). Yet, interestingly, this sex difference in preferences does not translate into a higher number of self-reported sexual partners. In fact, both men and women are similar in number of self-reported sexual partners (ANOVA, $F_{(1, 711)} = 0.61$, $P = 0.42$).

Overall, those who identify themselves as non-heterosexual (both 'homosexual' and 'bisexual(other)' categories) have a higher average number of self-reported sexual partners compared against heterosexuals (ANOVA, $F_{(2, 710)} = 9.72$, $P < 0.001$), are more likely to desire extra-pair sex (Table 1; Figure 2A), and are also more likely to believe in simultaneous love (Table 2; Figure 2B). This significance extends when sexual orientation is combined with gender (Table 1, Table 2; Figure 3). While those participants in the bisexual(other) category do express the overall highest tendency to desire extra-pair sex (including 100% of bisexual men), there are differences in this desire per gender in each sexuality category (*see* Figure 3A). More specifically, this high tendency to desire extra-pair sex is fairly consistent among both heterosexual men (84.2%) and homosexual men (79.4%). Whereas, there is a stronger difference between the women in different sexual orientation categories, with the lowest desire observed among heterosexual women (at 67%), relatively compared with high desires for extra-pair sex in homosexual women (87.5%) and bisexual women (88.2%) (*see* Figure 3A). Similarly, this disparity between sexual orientation when combined with gender is further observed in differences between participants' belief in simultaneous love (Figure 3B). While the higher proportion of belief in simultaneous love is seen in men in both heterosexual (62.1%)

and homosexual (76.5%) categories (compared with heterosexual women [48.9%] and homosexual women [37.5%]), this pattern is distinctly contrary in the 'bisexual(other)' category, where bisexual women express the highest belief in simultaneous love (81.6%) compared to a much lower tendency in bisexual men (51.2%) (Figure 3B).

DISCUSSION

This research provided a quantitative analysis investigating the multivariate basis and expressions of promiscuity desires in humans framed around sexual selection theory, while taking into account individual perception on love in the context of partner and sexual relationships. Based on the findings of this study, 84.5% of participants (including men and women across sexual orientation categories) express a desire for promiscuity. These results provide support to the hypotheses that there is a greater tendency in men to desire promiscuous matings in comparison to women (hypothesis i), and that individuals who identify themselves as non-heterosexual are more likely to desire promiscuous mating than heterosexual individuals (hypothesis iv). In contrast, these results failed to support the other hypotheses that a greater tendency exists in younger people to desire promiscuous matings in comparison to older generations (hypothesis ii), and that promiscuity is higher in those who have higher ratings of self-assessed attractiveness (hypothesis iii). Thus, these tests reject hypotheses (ii) and (iii).

In addition, a central aim of this study was to generalise forms of attraction under a single conceptual framework designed to fit sexual/partner-level interactions in humans, developed below (see also Figure 4).

The extent of promiscuity in humans

Supporting evolutionary theory and consistent with an extensive body of literature (Buss & Schmitt, 1993; Landolt *et al.*, 1995; Eastwick *et al.*, 2013), the findings from this study show that men express a greater (84.9% of participants) desire to engage in multiple relationships than women (71.2%). However, despite this higher desire for multiple sexual relationships, it appears men do not actually tend to gain extra sexual encounters, since numbers of self-reported sexual encounters are relatively similar between the sexes. This evidence suggests that men are potentially constrained, not only by social or religious values, but also by women,

in access to sexual relationships, perhaps unsurprisingly given that women are most often the deciders on whether to engage in sex (Kirkpatrick, 1982; Baumeister & Vohs, 2004). This pattern is suggestive to conform to Bateman's model of intense sexual selection on male competition as a result of female choice (Brown *et al.*, 2009).

The intensity of sexual selection is expressed through pressure on traits associated with maximising sexual reproduction, and determined by the likelihood of access to mates (e.g., as one sex becomes less frequent relative to the other, sexual selection intensifies on traits expressed in the more common sex) (Andersson, 1994; Shuster & Wade, 2003). As discussed above, attractiveness traits in humans strongly influence the chances of successfully gaining mating (Kirkpatrick, 1982; Lippa 2005;), with physical attractiveness and height being consistently demonstrated as the top traits in mate preferences (Buss, 1989; Barber, 1995; Schmitt, 2004). Interestingly, despite such emphasis on these attractiveness traits in the literature, these analyses revealed that self-assessed attractiveness is not an important mediator of desiring promiscuity. This finding could be due to limitations of the questionnaire design (as discussed below), and particularly with employing measures of self-assessed attractiveness. By asking participants to rate their own attractiveness might in fact differ greatly to a standardised or peer-reviewed rating of attractiveness, and hence reduce the reliability of the presented data (Swami, 2011). Therefore, it is suggested that reconsideration of questionnaire design would provide greater validity to these derived conclusions to further understand human behaviour.

In addition, these results revealed that age does not affect the desire for promiscuity. This finding could be due to limitations from unbalanced categories within the dataset, which creates over/under estimation bias of trends – a limitation that many human questionnaire datasets will inevitably encounter (Rea & Parker, 2014). However, it is important to note that age does not have a time-dependant effect on numbers of sexual relationships, given that at any age throughout life humans could increase their numbers of sexual partners. During earlier ages, when constraints from responsibilities are lowest and access to mates is perceived as highest (Buss, 1994), selection pushes for finding the highest quality mates, particularly for young women whose cost of pregnancy is higher (Borgerhoff Mulder, 2009). However, by later ages, the majority of people have experienced long term relationships and are more likely to have achieved raising children (i.e., achieved sexual fitness). In these later age groups, the desire for promiscuity remains consistently high, and sexual selection may experience

intensification throughout reproductively viable ages (Schaffer, 1974). This finding provides additional support for the idea that individual humans can fluctuate between mating strategies throughout progression of life, depending on resource and environmental constraints, highlighting the complexities of human sexual interactions (Roberts & Havlíček, 2013; Stewart-Williams & Thomas, 2013).

A logical assumption when investigating factors that predict the likelihood of desires for promiscuity, is that as the number of sexual encounters increases so will the likelihood of promiscuity (Shuster & Wade, 2003). This is an important feature driving species towards polygamous mating systems, given that selection is likely to favour genetic variation in broods, which in turn contributes to the chances of more successful offspring (Yasui, 1998; Tregenza & Wedell, 2002; Pincheira-Donoso & Hunt, 2016). With high genetic diversity, broods are better equipped to possess capabilities to respond and survive to environmental pressures. Therefore, selection promotes promiscuity to be selected and passed onto subsequent generations (Yasui, 1998; Tregenza & Wedell, 2000). However, these adaptive benefits of multiple mating also face many costly trade-offs, such as decreased longevity (Slayter, *et al*., 2012; Scharf, *et al*., 2015), again highlighting the multidimensionality and complexities of sexual interactions.

One of the strongest findings in this study is that individuals who identify themselves as non-heterosexual have a greater tendency towards desiring promiscuity and are more likely to believe in simultaneous love than heterosexual individuals (*see* Figure 2; Table 1 and Table 2). This finding supports a growing body of literature investigating the influence of sexual orientation on sexual desires from an evolutionary perspective (Phellas, 2012). This study found that individuals who identify as 'Bisexual(other)' have the greatest tendency towards desire for promiscuity and simultaneous love, when compared against exclusively homosexual and heterosexual individuals (Figure 3). This finding suggests that this phenomenon may be explained by the nature of individuals who identify as bisexual, who are more sexually fluid, and have a greater tendency to consider a wider diversity of sexual attraction and are less resistant to possibilities of polygamy and multiple relationships, compared to individuals who have an exclusive attraction to one sex (Diamond, 2008; Klesse, 2012). However, the tendency to desire promiscuity and simultaneous love is still relatively strong in individuals who identify themselves as homosexual, in comparison to the lower tendencies shown in heterosexual individuals. Therefore, it appears that non-heterosexual individuals could be less

constrained by the fitness costs of polygamy that typically constrain heterosexual relationships, such as choosy females. Given the strong effect of gender on promiscuous desires and sexual attraction within different sexualities, this study shows that coupling gender and sexual orientation (Figure 3) is essential to further dissect the spectrum of sexual orientation and sexual identity in human relationships and sexual desires (Schmit, 2007; Lippa, 2007). These findings further highlight the diversity across and within different sexualities in our highly socially complex species.

This complex interaction of factors influencing human sexual interactions is a prime example of how mating systems are context-dependant (Shuster & Wade, 2003). Humans are able to adopt several mating strategies and function to maintain relationships and sexual interactions (Stewart-Williams & Thomas, 2013; Wlodarski *et al.*, 2015). There is much evidence for interspecies variation, sexual fluidity (e.g., bisexuality) (Diamond, 2008), which hence suggests that mating systems are flexible, to allow reaction to environmental change, and to enhance chances of adaptive responses (Roberts & Havlíček, 2013). Thus, sexual attraction in any form is consistent as a strong evolutionary principle.

A generalised framework for a concept of attraction

At the more conceptual level, this study presents a generalisation of the multiple forms of attraction under a single conceptual framework designed to fit sexual/partner-level interactions in humans. This conceptual framework is here proposed to be materialised under the metaphor of an 'attraction landscape' (*see* Figure 4). This landscape suggests that attraction can be described as a surface built based on the relationship between variation in the axes 'sexual motivation' and 'companionship'. These simple components of attraction intertwine and are highly variable, meaning that each relationship can be uniquely placed on different points on the surface of the attraction landscape (Figure 4). One of the fundamental advantages offered by this theoretical framework is that it provides a dynamical surface where individuals can drift depending on their positions along each axis. That is, individuals will drift on the surface as they displace along the axes x and y dimensions. Therefore, this attraction landscape offers a surface on which individuals can be located as a result of their level of attraction, and also can show how these emotions can change over the course of a relationship and over the course of evolution, when considering their positions at different historical and cultural influences. Consequently, this landscape metaphor overcomes previous limitations of

other theories (Acker and Davis, 1992), such as the Triangular Theory of Love (Sternberg, 1986), and Fisher's three stages of love (Fisher, 2000), which attempts to categorise all relationships into a linear context (which rather unrealistically pictures attraction as based on *either* sexual motivation *or* a need for companionship). By contrast, this conceptual framework allows any degree of relationship to be placed on the landscape, incorporating the ability for movement to highlight the dynamic and highly variable nature of attraction.

Despite current limitations, the development of this attraction landscape provides a greater depth and expanded perspective of love for this field of research. Thus, the model presented in this research can offer an alternative to solve at least in part the limitations of previous attraction models where dynamic changes over time are not possible, making them unrealistic and rather 'static'. Conclusively, by producing this conceptual framework, this thesis attempted to formalise a novel approach to quantify the complex variety of human sexual relationships.

Sex and love in human mating

The relationship between sexual desire and love is highly variable, but they are not always mutually exclusive. In humans, where such casual encounters exist, individuals can often limit their attachment to a casual mate, given the intrinsic lack of commitment, and often when choosing casual mates humans tend to be less choosy or compromise on qualities they would favour with a longer term partner (Kokko *et al.*, 2003; Quinlan, 2008). However, when seeking a committed relationship, the expression of love becomes an important factor in maintaining the success of a relationship and mutual parental investment, and the level of choosiness increases (Trivers, 1972; Kirkpatrick, 1982; Zeifman & Hazan, 2008). With much research on sexual interactions, the emphasis is on the differential ability of individuals to engage in sex for simply the purposes of gaining reproduction (i.e., an intrinsically fitness-driven behaviour) (Trivers, 1972; Parker & Pizzari, 2015). This research may ignore the potential for other forces of attraction involving commitment, depending on the mating system, since such expression of attraction can impose higher costs than benefits (e.g., in polygamous systems) (Miller *et al.*, 2005). Human societies tend to link 'love' with an expression of attractive force mediated by commitment, while the landscape proposed in this study (Figure 4) suggests that such expressions of attraction are the result of the interaction between two interacting dimensions of attraction called 'sexual motivation' and 'companionship'. Interestingly, this research

revealed that in humans, love can be experienced not just from one individual exclusively to another, but instead there is a high tendency for human individuals experiencing love for more than one potential partner simultaneously. Several pair-bonds make it possible to sustain multiple mating relationships, promoting increased benefits of maximising reproductive fitness (Miller *et al.*, 2005; Zeifman & Hazan, 2008).

Ultimately, and according to the 'attraction landscape' presented above (Figure 4), sexual motivation and commitment are simply different positions on the surface of a generalised expression of attraction that can drift from more sexually or committed extremes depending on differing stages of relationships within humans, which can express over time within the course of the same relationship, among different cultures or ages of the same cultures if their social systems have changed historically.

Limitation of methodological approach

Based on reflective analyses, a caveat inherent to this (and other questionnaire-based approaches) research is the accuracy and especially the 'universality' of questionnaire design, and it is suggested that if this study were to be replicated it would be of greater benefit to revise this questionnaire design and correct for bias of unequal responses per category. Specifically, this could be achieved by removing the ambiguous questions and instead expanding the scope of optional answers for remaining questions, in order to increase accuracy of quantitative measures to better distinguish attitude and desires from actual behaviours. Further data analyses could expand from testing individual and categorical differences to include testing relationships between variables.

Another limitation of this study is the lack of cultural diversity from the data collection. This study has primarily focused on investigating the sexual relationships of humans from predominately Western culture (mainly UK and USA). This provides limits to the ability to generalise findings from this study to all humans. Therefore, it is important to consider cross-cultural effects and how cultural influences on human desires and attitudes, which limits the ability to draw inferences from these data. This is especially valuable when using these results to develop a unified theory of love, therefore it would be greatly beneficial to expand the scope of questionnaire distribution to gain evidence of the effects of promiscuous desires and attitudes towards multiple love from participants with different cultural backgrounds.

Conclusions

In conclusion, this research has quantified how humans express a high extent of desires for promiscuous mating and belief in simultaneous love. However, notably, it is highlighted that humans are adaptable and there is high variation within sexual interactions, to allow the freedom of experiencing many types of attraction. This thesis has attempted to be a starting point towards a generalised conceptualisation of attraction in humans while taking into account the multiple components of promiscuity and love, which express very strongly and visibly in humans. More specifically, future research could formulate where individuals can fit onto this 'landscape', using precise and measurable calculations. Consequently, this will provide a tool to allow the generation of much richer sets of predictions on how sexual selection operates on human sexual interactions, particularly including how such variations occur over an individual's lifetime and across different human populations. There is also a strong need to produce this scientific progress in our understanding of love, crucial for meaningful dialogue and benefitting knowledge towards understanding the complexities of human relationships.

REFERENCES

Acker, M. & Davis, M.H. (1992) Intimacy, passion and commitment in adult romantic relationships: A test of the triangular theory of love. *Journal of Social and Personal Relationships*, **9**, 21-50.

Andersson, M.B. (1994) *Sexual selection*. Princeton University Press.

Arnqvist, G. & Rowe, L. (2005) *Sexual conflict.* Princeton University Press: Princeton.

Bailey, J. M., Gaulin, S., Agyei, Y., & Gladue, B. A. (1994). Effects of gender and sexual orientation on evolutionarily relevant aspects of human mating psychology. *Journal of personality and social psychology*, **66**, 1081.

Barber, N. (1995) The evolutionary psychology of physical attractiveness: Sexual selection and human morphology. *Ethology and Sociobiology*, **16**, 395-424.

Baumeister, R.F. & Vohs, K.D. (2004) Sexual economics: Sex as female resource for social exchange in heterosexual interactions. *Personality and Social Psychology Review*, **8**, 339-363.

Bell, G. (2012) *Selection: the mechanism of evolution*. Springer Science & Business Media.

Borgerhoff Mulder, M. (2009) Serial monogamy as polygyny or polyandry?: marriage in the tanzanian pimbwe. *Human Nature*, **20**, 130-50.

Brehm, S. S. (1985). *Intimate relationships*. New York: Random House.

Brown, G.R., Laland, K.N. & Borgerhoff Mulder, M. (2009) Bateman's principles and human sex roles. *Trends in Ecology & Evolution*, **24**, 297-304.

Buss, D.M. (1988) The evolution of human intrasexual competition: tactics of mate attraction. *Journal of personality and social psychology*, **54**, 616-628.

Buss, D.M. (1989) Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and brain sciences*, **12**, 1-14.

Buss, D.M. (1994) *The evolution of desire: Strategies of human mating*. Basic books.

Buss, D.M. & Barnes, M. (1986) Preferences in human mate selection. *Journal of personality and social psychology*, **50**, 559-570.

Buss, D.M. & Schmitt, D.P. (1993) Sexual strategies theory: an evolutionary perspective on human mating. *Psychological review*, **100**, 204-232.

Clutton-Brock, T.H. (1989) Review lecture: mammalian mating systems. *Proceedings of the Royal Society of London B: Biological Sciences*, **236**, 339-372.

Clutton-Brock, T.H. & Parker, G.A. (1992) Potential reproductive rates and the operation of sexual selection. *Quarterly Review of Biology*, 437-456.

Cornwallis, C.K. & Uller, T. (2010) Towards an evolutionary ecology of sexual traits. *Trends in Ecology & Evolution*, **25**, 145-152.

Corporation, I. (2013) IBM SPSS Statistics for Windows, Version 22.0. In. IBM Corp, Armonk, NY.

Darwin, C. (1871) *The Descent of Man and Selection in Relation to Sex*. Murray, London.

Dawkins, R. (2006) *The selfish gene*. Oxford University Press.

Diamond, L.M. (2008) *Sexual fluidity*. Wiley Online Library.

Dixson, A.F. (2009) *Sexual selection and the origins of human mating systems*. Oxford University Press.

Dunbar, R., Lycett, J. & Barrett, L. (2005). *Evolutionary Psychology: A Beginner's Guide.* Oneworld Publications: Oxford.

Durrant. R. and Ward, T. (2011). Evolutionary explanations in the social and behavioral sciences: Introduction and overview. *Aggression and Violent Behavior*, **16**, 361-370.

Eastwick, P.W., Luchies, L.B., Finkel, E.J. & Hunt, L.L. (2013) The predictive validity of ideal partner preferences: A review and meta-analysis.

Emlen, S.T. & Oring, L.W. (1977) Ecology, sexual selection, and the evolution of mating systems. *Science*, **197**, 215-223.

Fehr, B., & Russell, J. A. (1991). Concept of love viewed from a prototype perspective. *Journal of Personality and Social Psychology*, **60**, 425-438.

Finkel, E.J. & Eastwick, P.W. (2015) Attachment and pairbonding. *Current Opinion in Behavioral Sciences*, **3**, 7-11.

Fisher, H. (2000) Lust, attraction, attachment: Biology and evolution of the three primary emotion systems for mating, reproduction, and parenting. *Journal of Sex Education and Therapy*, **25**, 96-104.

Fisher, H. (2004) *Why we love: The nature and chemistry of romantic love*. Macmillan.

Fisher, T. D., Davis, C. M., Yarber, W. L., & Davis, S. L. (2010). *Handbook of Sexuality-Related Measures*. New York: Routledge.

Foster, K.R., Wenseleers, T. & Ratnieks, F.L. (2006) Kin selection is the key to altruism. *Trends in Ecology & Evolution*, **21**, 57-60.

Gangestad, S.W. & Simpson, J.A. (2000) The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and brain sciences*, **23**, 573-587.

Geary, D.C., Bailey, D.H. & Oxford, J. (2011) Reflections on the human family. *The Oxford handbook of evolutionary family psychology*, 365-385.

Glassenberg, A. N., Feinberg, D. R., Jones, B. C., Little, A. C., & DeBruine, L. M. (2010). Sex-dimorphic face shape preference in heterosexual and homosexual men and women. *Archives of Sexual Behavior*, **39**, 1289-1296.

Glick, P.C. (1984) Marriage, Divorce, and Living Arrangements Prospective Changes. *Journal of family issues*, **5**, 7-26.

Greiling, H. & Buss, D.M. (2000) Women's sexual strategies: the hidden dimension of extra-pair mating. *Personality and individual Differences*, **28**, 929-963.

Hadfield, J.D. (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, **33**, 1-22.

Harcourt, A. & Stewart, K. (2007) *Gorilla society: conflict, compromise, and cooperation between the sexes.* Chicago University Press.

Harcourt, A.H., Harvey, P.H., Larson, S.G. & Short, R.V. (1981) Testis weight, body weight and breeding system in primates. *Nature*, **293**, 55-7.

Hatfield, E. & Sprecher, S. (1986). Measuring passionate love in intimate relations. *Journal of Adolescence*, **9**, 383-410.

Hazan, C. & Shaver, P. (1987) Romantic love conceptualized as an attachment process. *Journal of personality and social psychology*, **52**, 511-524.

Henrich, J., Boyd, R. & Richerson, P.J. (2012) The puzzle of monogamous marriage. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 657-669.

Hervé, M. (2015) Diverse basic statistical and graphical functions. In. CRAN-R

Hrdy, S.B. (2006) 7 Empathy, Polyandry, and the Myth of the Coy Female. *Conceptual issues in evolutionary biology*, 131.

Jackson, J.J. & Kirkpatrick, L.A. (2007) The structure and measurement of human mating strategies: Toward a multidimensional model of sociosexuality. *Evolution and Human Behavior*, **28**, 382-391.

Jennions, M.D. & Petrie, M. (2000) Why do females mate multiply? A review of the genetic benefits. *Biological Reviews of the Cambridge Philosophical Society*, **75**, 21-64.

Kirkpatrick, M. (1982) Sexual selection and the evolution of female choice. *Evolution*, **36**, 1-12.

Klesse, C. (2012). *The spectre of promiscuity: Gay male and bisexual non-monogamies and polyamories*. Ashgate Publishing, Ltd.

Kokko, H. & Jennions, M.D. (2008) Parental investment, sexual selection and sex ratios. *Journal of evolutionary biology*, **21**, 919-948.

Kokko, H., Brooks, R., Jennions, M.D. & Morley, J. (2003) The evolution of mate choice and mating biases. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **270**, 653-664.

Laland, K. N. & Brown, G. R. (2011). *Sense and Nonsense: Evolutionary perspectives on human behaviour* (2nd edition). Oxford University Press: Oxford.

Landolt, M.A., Lalumière, M.L. & Quinsey, V.L. (1995) Sex differences in intra-sex variations in human mating tactics: An evolutionary approach. *Ethology and Sociobiology*, **16**, 3-23.

Lippa, R.A. (2009) Sex differences in sex drive, sociosexuality, and height across 53 nations: Testing evolutionary and social structural theories. *Archives of Sexual Behavior*, **38**, 631-651.

Little, A.C., Burriss, R.P., Petrie, M., Jones, B.C. & Roberts, S.C. (2013) Oral contraceptive use in women changes preferences for male facial masculinity and is associated with partner facial masculinity. *Psychoneuroendocrinology*, **38**, 1777-1785.

Little, A. C., & Mannion, H. (2006). Viewing attractive or unattractive same-sex individuals changes self-rated attractiveness and face preferences in women. *Animal Behaviour*, **72**, 981-987.

Low, B.S. (1988) Measures of polygyny in humans. *Current Anthropology*, 189-194.

Marlowe, F. (2000) Paternal investment and the human mating system. *Behavioural Processes*, **51**, 45-61.

Morgan, C. L. (1903). *An introduction to comparative psychology*, 2nd edition. W. Scott: London.

Miller, G. (2011) *The mating mind: How sexual choice shaped the evolution of human nature*. Anchor.

Miller, L.C., Pedersen, W.C. & Putcha-Bhagavatula, A. (2005) Promiscuity in an evolved pair-bonding system: Mating within and outside the Pleistocene box. *Behavioral and Brain Sciences*, **28**, 290-291.

Nosil, P. (2012) *Ecological speciation*. Oxford University Press.

Parker, G. (2006) Sexual conflict over mating and fertilization: an overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **361**, 235-259.

Parker, G. & Pizzari, T. (2015) Sexual Selection: The Logical Imperative. *Current Perspectives on Sexual Selection* (ed. by T. Hoquet), pp. 119-163. Springer.

Penke, L. & Asendorpf, J.B. (2008) Beyond global sociosexual orientations: a more differentiated look at sociosexuality and its effects on courtship and romantic relationships. *Journal of personality and social psychology*, **95**, 1113.

Perls, T.T., Alpert, L. & Fretts, R.C. (1997) Middle-aged mothers live longer. *Nature*, **389**, 133-133.

Phellas, C. N. (2012). *Researching Non-heterosexual Sexualities*. Ashgate Publishing, Ltd.

Pincheira-Donoso, D. & Hunt, J. (2015) Fecundity selection theory: concepts and evidence. *Biological Reviews (In Press)*.

Post, S. (2003) *Research on Altruism & Love*. Templeton Foundation Press.

Quinlan, R.J. (2008) Human pair-bonds: Evolutionary functions, ecological variation, and adaptive development. *Evolutionary Anthropology: Issues, News, and Reviews*, **17**, 227-238.

Rea, L.M. & Parker, R.A. (2014) *Designing and conducting survey research: A comprehensive guide*. John Wiley & Sons.

Reynolds, J.D. (1996) Animal breeding systems. *Trends in Ecology & Evolution*, **11**, 68-72.

Roberts, S.C. & Havlíček, J. (2013) Humans are dunnocks, not peacocks: on cause and consequence of variation in human mating strategies. *Psychological Inquiry*, **24**, 231-236.

Roberts, S.C., Cobey, K.D., Klapilová, K. & Havlíček, J. (2013) An evolutionary approach offers a fresh perspective on the relationship between oral contraception and sexual desire. *Archives of sexual behavior*, **42**, 1369-1375.

Scelza, B.A. (2011) Female choice and extra-pair paternity in a traditional human population. *Biology Letters*, rsbl20110478.

Schäfer, S. (1977). Sociosexual behavior in male and female homosexuals: A study in sex differences. *Archives of Sexual Behavior*, **6**, 355-364.

Schaffer, W.M. (1974) Selection for optimal life histories: the effects of age structure. *Ecology*, 291-303.

Scharf, I., Feldman, A., Novosolov, M., Pincheira-Donoso, D., Das, I., Böhm, M., Uetz,. P., Torres-Caravjal, O., Bauer, A., Roll, U. & Meiri, S. (2015). Late bloomers and baby boomers: ecological drivers of longevity in squamates and the tuatara. *Global Ecology and Biogeography*, **24**, 396-405.

Schmitt, D.P. (2003) Universal sex differences in the desire for sexual variety: tests from 52 nations, 6 continents, and 13 islands. *Journal of personality and social psychology*, **85**, 85.

Schmitt, D.P. (2004) The Big Five related to risky sexual behaviour across 10 world regions: Differential personality associations of sexual promiscuity and relationship infidelity. *European Journal of Personality*, **18**, 301-319.

Schmitt, D.P. (2005) Sociosexuality from Argentina to Zimbabwe: A 48-nation study of sex, culture, and strategies of human mating. *Behavioral and Brain Sciences*, **28**, 247-275.

Schmitt, D. P. (2007). Sexual strategies across sexual orientations: How personality traits and culture relate to sociosexuality among gays, lesbians, bisexuals, and heterosexuals. *Journal of Psychology & Human Sexuality*,**18**, 183-214.

Schmitt, D.P., Realo, A., Voracek, M. & Allik, J. (2008) Why can't a man be more like a woman? Sex differences in Big Five personality traits across 55 cultures. *Journal of personality and social psychology*, **94**, 168.

Shaver, P.R., Morgan, H.J. & Wu, S. (1996) Is Love a" Basic" Emotion? *Personal Relationships*, **3**, 81-96.

Shuster, S.M. & Wade, M.J. (2003) *Mating systems and strategies*. Princeton University Press.

Simpson, J.A. & Gangestad, S.W. (1991) Individual differences in sociosexuality: evidence for convergent and discriminant validity. *Journal of personality and social psychology*, **60**, 870.

Slatyer, R. A., Mautz, B. S., Backwell, P. R., & Jennions, M. D. (2012). Estimating genetic benefits of polyandry from experimental studies: a meta-analysis. *Biological Reviews*, **87**, 1-33.

Small, M.F. (1995) *What's Love Got to Do with It?: The Evolution of Human Mating*. Anchor Books.

Stewart-Williams, S. & Thomas, A.G. (2013) The ape that thought it was a peacock: Does evolutionary psychology exaggerate human sex differences? *Psychological Inquiry*, **24**, 137-168.

Swami, V. (2011). *Evolutionary psychology: A critical introduction*. Wiley-Blackwell.

Symons, D. (1980) The evolution of human sexuality revisited. *Behavioral and Brain Sciences*, **3**, 203-214.

Székely, T., Moore, A.J. & Komdeur, J. (2010) *Social behaviour: genes, ecology and evolution*. Cambridge University Press.

Team, R.C. (2014) *R: A language and environment for statistical computing*. New York.

Tregenza, T. (2003) Evolution: The battle between the sexes. *Nature*, **423**, 929-930.

Tregenza, T. & Wedell, N. (2000) Genetic compatibility, mate choice and patterns of parentage: invited review. *Molecular Ecology*, **9**, 1013-1027.

Tregenza, T. & Wedell, N. (2002) Polyandrous females avoid costs of inbreeding. *Nature*, **415**, 71-73.

Trivers, R. (1972) Parental investment and sexual selection. *Sexual Selection & the Descent of Man, Aldine de Gruyter, New York*, 136-179.

Trivers, R.L. (1971) The evolution of reciprocal altruism. *Quarterly review of biology*, 35-57.

Voracek, M. (2005). Shortcomings of the Sociosexual Orientation Inventory: Can psychometrics inform evolutionary psychology? *Behavioral and Brain Sciences*, **28**, 296-297.

Wade, M.J. & Arnold, S.J. (1980) The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. *Animal Behaviour*, **28**, 446-461.

Wlodarski, R. & Dunbar, R.I. (2014) The effects of romantic love on mentalizing abilities. *Review of General Psychology*, **18**, 313.

Wlodarski, R., Manning, J. & Dunbar, R.I.M. (2015) *Stay or stray? Evidence for alternative mating strategy phenotypes in both men and women*.

Yasui, Y. (1998) The genetic benefits' of female multiple mating reconsidered. *Trends in Ecology & Evolution*, **13**, 246-250.

Zeifman, D. & Hazan, C. (2008) *Pair bonds as attachments: Reevaluating the evidence*. In: *Handbook of attachment: Theory, research, and clinical applications* (2nd ed.) Guilford Press.

FIGURES AND TABLES

Table 1. Summary of results from MCMC GLMM analyses (*see Methods for more details*), testing whether multiple factors (gender, age, self-assessed attractiveness rating (selfatt), sexual orientation (sexor) and number of sexual partners (sexenc)) influences the desire for extra-pair sex. Significant relationships are shown in bold and italics.

	Posterior Probability Mean	95% CI		Effective sample	*P*
		Lower	Upper		
(Intercept)	-0.00841	-0.89581	0.852578	8.929	0.97473
gender	0.1285	0.94926	0.669919	18.279	***0.05143***
age	0.79274	0.05724	0.526695	5.156	0.36581
selfatt	0.16094	-0.29009	0.52214	6.539	0.64857
sexor	0.003428	-0.12889	0.120756	12.362	***0.03571***
sexenc	-0.06842	-0.32625	0.320881	3.807	0.73143
gender:age	-0.03317	-0.17258	0.112046	7.702	0.48857
gender:selfatt	0.021925	-0.04328	0.084785	9.476	0.61714
gender:sexor	-0.03306	-0.23036	0.122225	12.4	***0.00429***
gender:sexenc	-0.06976	-0.22011	0.058958	5.265	0.30857
age:selfatt	-0.0193	-0.04205	-0.00015	10.213	0.05529
age:sexor	-0.03756	-0.10928	0.02513	7.345	0.26571
age:sexenc	-0.00346	-0.04964	0.034725	5.962	0.91429
selfatt:sexor	-0.0021	-0.0545	0.046912	4.995	0.97429
selfatt:sexenc	0.019502	-0.00162	0.051967	5.81	0.12571
sexor:sexenc	0.005177	-0.04275	0.053492	10.636	0.86286

Table 2. Summary of results from MCMC GLMM analyses (*see Methods for more details*), testing whether multiple factors (gender, age, self-assessed attractiveness rating (sexatt), sexual orientation (sexor) and number of sexual partners (sexenc)) influences the belief of simultaneous love. Significant relationships are shown in bold and italics.

	Posterior Probability Mean	95% CI		Effective sample	*P*
		Lower	Upper		
(Intercept)	-0.00921	-0.99436	0.952108	9.969	0.93143
gender	-0.69435	-0.73245	0.75326	15.279	***0.0596***
age	0.23891	0.49271	0.425493	2.15	0.78571
selfatt	0.6548	-0.18759	0.168956	8.322	0.82571
sexor	0.04694	-0.29009	0.52214	11.539	***0.03457***
sexenc	-0.06783	-0.39402	0.375481	3.638	0.54923
gender:age	-0.54298	-0.16376	0.10532	7.873	0.45673
gender:selfatt	0.02165	-0.04643	0.088653	9.487	0.65424
gender:sexor	-0.03654	-0.25673	0.126535	14.6	***0.04093***
gender:sexenc	-0.07423	-0.24324	0.054932	5.2432	0.34392
age:selfatt	-0.02043	-0.04256	-0.03325	9.273	0.06729
age:sexor	-0.04529	-0.189421	0.04321	7.393	0.28482
age:sexenc	-0.05632	-0.05432	0.049723	4.974	0.92603
selfatt:sexor	-0.03456	-0.06042	0.053821	4.890	0.9843
selfatt:sexenc	0.021093	-0.00144	0.059025	5.64	0.1361
sexor:sexenc	0.005032	-0.04932	0.06353	9.365	0.9012

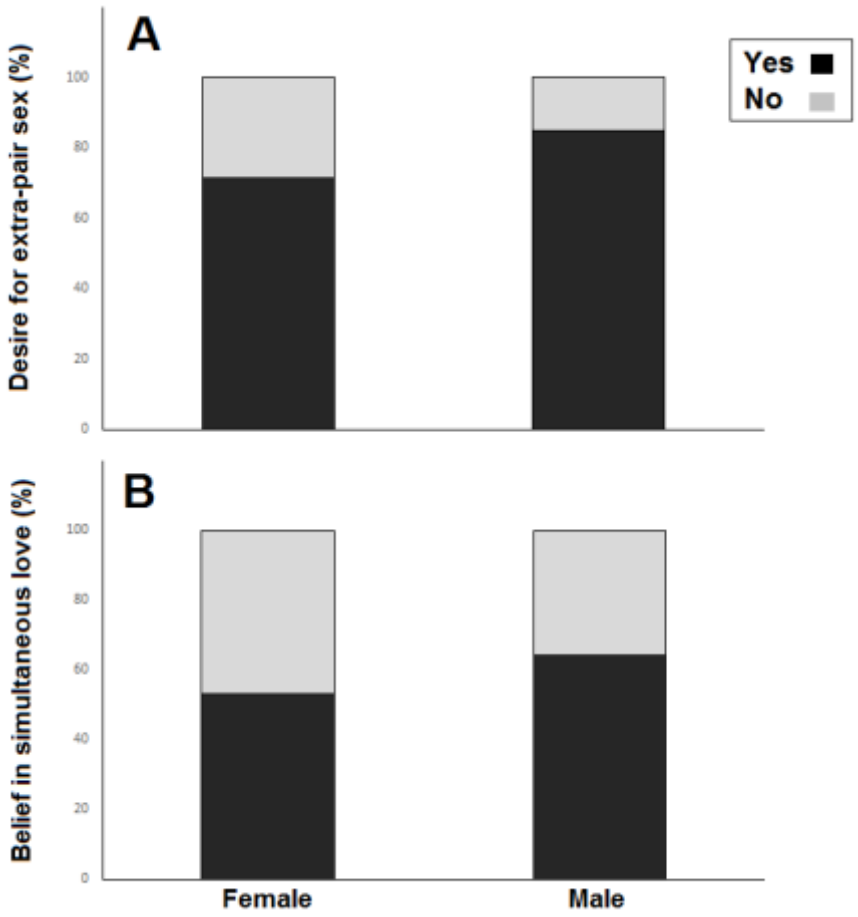

Figure 1. Proportion of female and male participants' responses for (**A**) their desire to engage in extra-pair sex whilst in a relationship, and (**B**) their belief in loving more than one person simultaneously. Out of the total category sample, the proportion of participants who responded with 'Yes' to each question is represented in black and the proportion of participants who responded with 'No' to each question is represented in light grey.

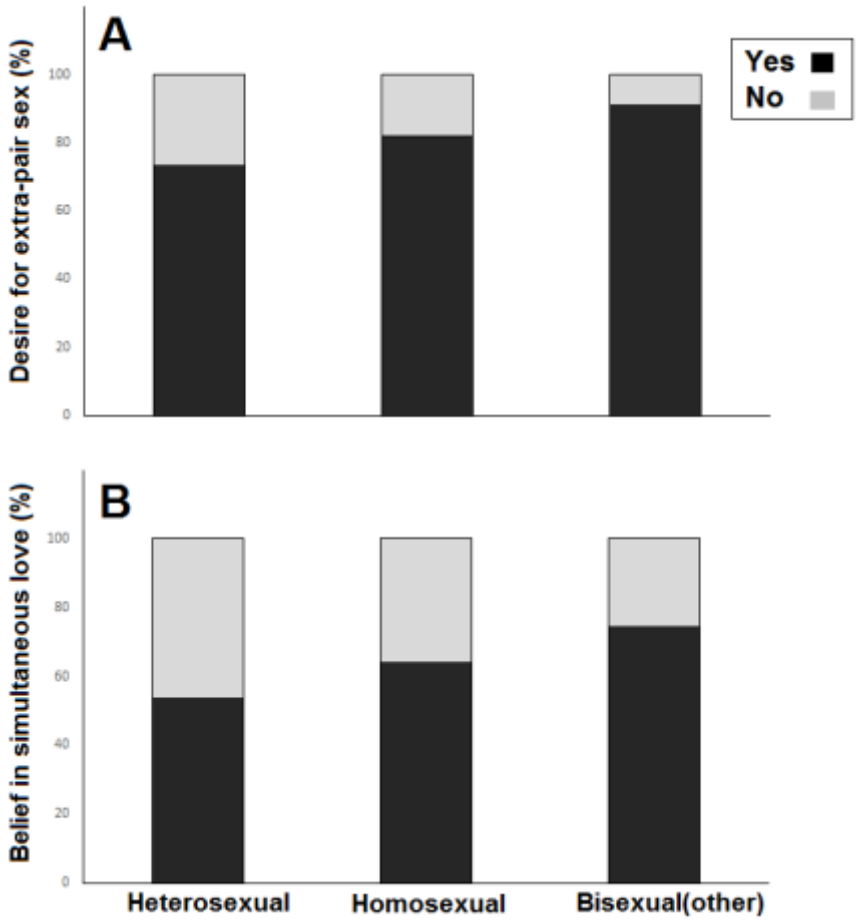

Figure 2. Proportion of participants' responses per sexual orientation category for (**A**) their desire to engage in extra-pair sex whilst in a relationship, and (**B**) their belief in loving more than one person simultaneously. Out of the total category sample, the proportion of participants who responded with 'Yes' to each question is represented in black and the proportion of participants who responded with 'No' to each question is represented in light grey.

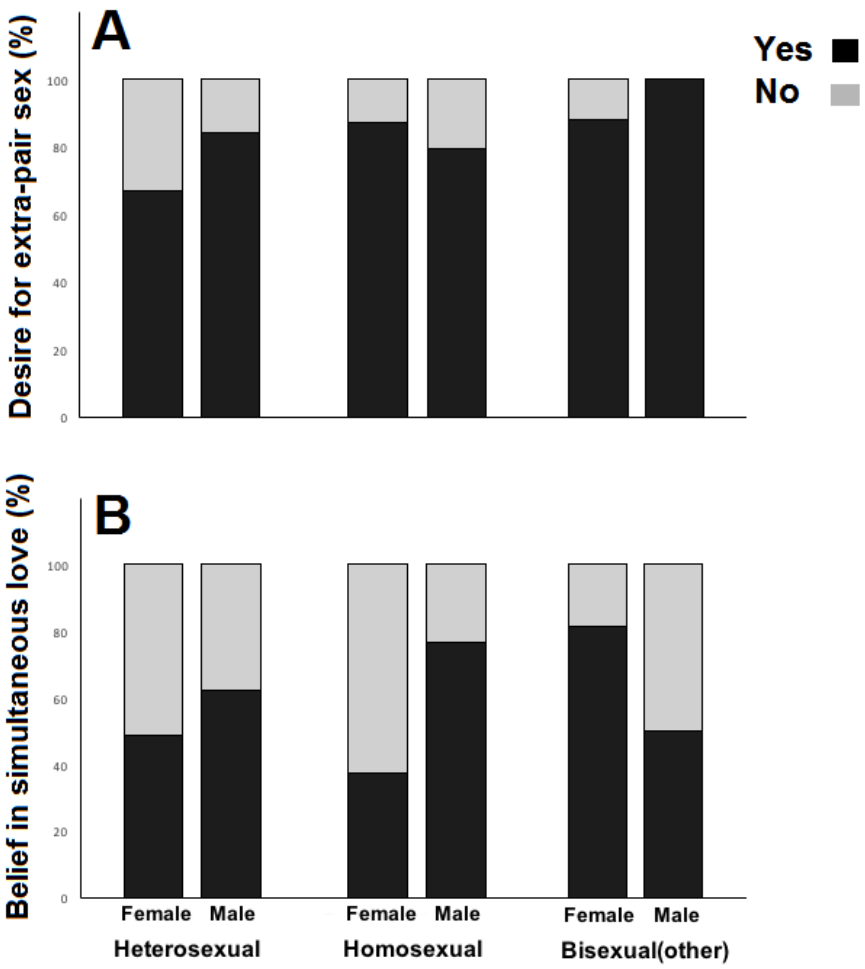

Figure 3. Proportion of participants' responses per gender and sexual orientation category for (**A**) their desire to engage in extra-pair sex whilst in a relationship, and (**B**) their belief in loving more than one person simultaneously. Out of the total category sample, the proportion of participants who responded with 'Yes' to each question is represented in black and the proportion of participants who responded with 'No' to each question is represented in light grey.

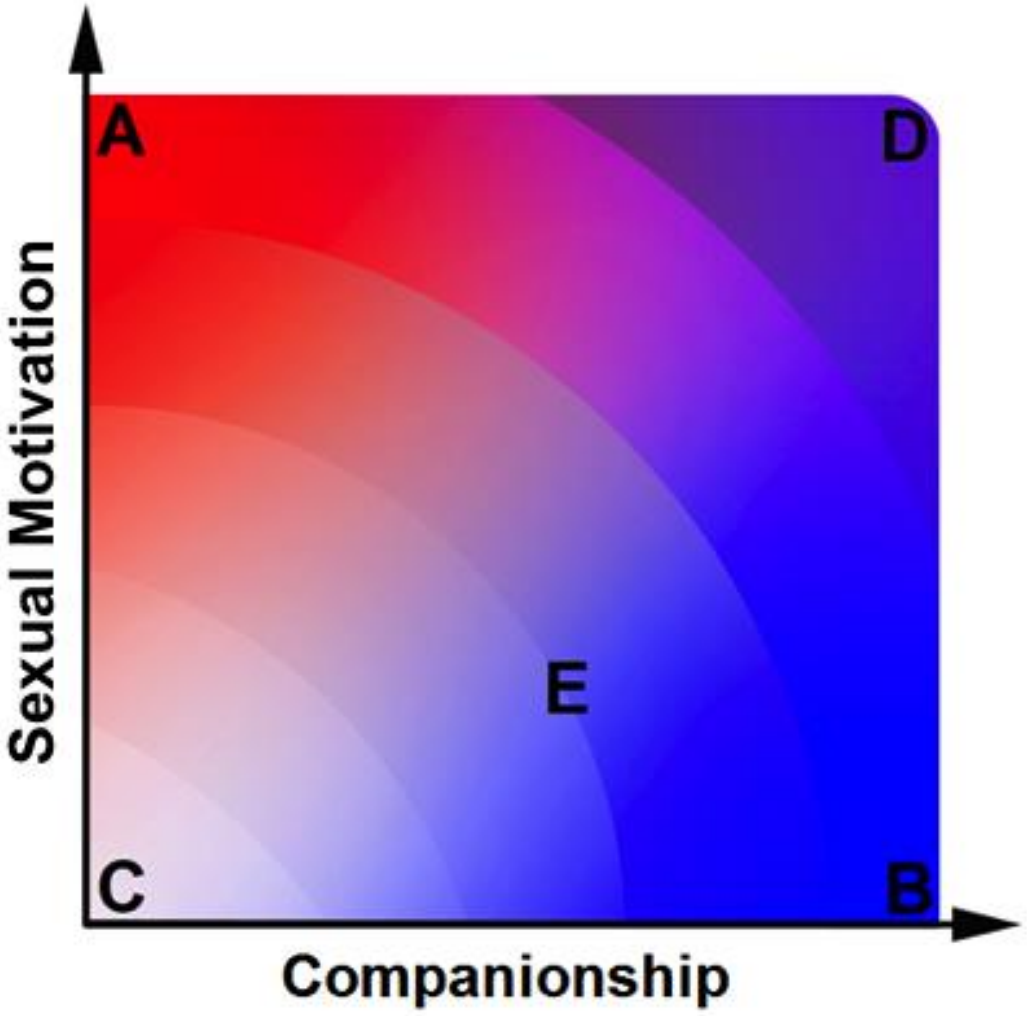

Figure 4. Depiction of the 'Attraction Landscape'. Theoretical diagram encompassing the landscape where relationships can be placed, along axes dimensions of 'sexual motivation' (red) and 'companionship' (blue). As examples to illustrate the workings of such landscape; **A** describes high levels of sexual motivation with no companionship feelings, often referred to as 'infatuation love', while, in contrast, **B** represents high levels of companionship with no sexual motivation. **C** describes low levels of both parameters, perhaps indicative of early relationships. **D** (purple) represents the combination of high extremes for both parameters, deemed 'consummate love' or 'true love'. Finally, **E** represents an intermediate level of companionship with fairly low levels of sexual motivation, and illustrates the capability of movement across this landscape.

SUPPLEMENTARY MATERIAL

Supplementary material S1. Copy of questionnaire approved by College of Science Research Degrees Board (University of Lincoln UK), including questionnaire questions and information for participants.

Be Part of Research on Sex & Love

Thank you for taking part in this 7 minute online questionnaire, which aims to investigate how sexual selection has influenced sex and love dynamics in humans, as part of research being conducted at the University of Lincoln (UK).

Your participation is completely anonymous and you can withdraw at any time.

If you have any queries, please feel free to contact the leading researcher Lilly Harvey (lharvey@lincoln.ac.uk).

For more information on what is expected of you as a participant, please select "Yes" below.

Else, by clicking "Continue", you are consenting to participate in this research.

Information for Participants

This questionnaire aims to investigate how evolutionary theories and mechanisms of sexual selection have influenced sex and love dynamics in humans, as part of research being conducted at the University of Lincoln (UK). If you agree to take part, you will answer demographic questions, such as your age, gender, sexual orientation etc., and research questions about your opinions on and experiences of sexual and romantic attraction. It is important to answer these questions with complete honesty and do not overthink your answers. It will only take approximately 7 minutes to complete this questionnaire. This questionnaire is completely anonymous, and any personal information or answers you give will be kept confidential. Your participation is voluntary, therefore you can withdraw from participating in this research at any time by simply exiting the questionnaire. This questionnaire poses no risks beyond what one would encounter in day-to-day-living and with responding to any online questionnaire. While you may feel uncomfortable when being asked questions about your gender, sexual orientation, sexual and romantic attraction, or sexual and romantic history, you may always choose not to answer any of the questions in this questionnaire.

However, please do be aware that your answers are completely anonymous, therefore we hope this reduces any anxieties and allows you to answer all questions honesty and to enjoy the process of contributing to research. In consideration of all of the above, you can be fully committed to consenting to participate in this research by clicking "Continue" below.

Thank you for agreeing to be part of this research! Note that in this questionnaire we are defining "love" as: the attractions and/or affections you would have for a partner figure only (rather than maternal or parental affections). Please keep this in consideration to answer questions appropriately.

1. Which age category do you fit into?

o 18 - 24

o 25 - 30

o 31 - 40

o 41 - 50

o 51 - 59

o 60 +

2. What is your gender?

o Female

o Male

o Prefer not to say

o Other:

3. Where do you live?

o UK

o USA

o Other:

4. What is your height?

Please round to the nearest appropriate measure

o ≤ 5"0 (≤ 154cm)

o 5"1 - 5"4 (155 - 164cm)

o 5"5 - 5"8 (165 - 174cm)

o 5"9 - 6"0 (175 - 184cm)

o 6"1+ (185cm+)

5. What is your sexual orientation?

o Heterosexual

o Homosexual

o Prefer not to say

o Other:

6. What is your current relationship status?

o Single

o In a casual relationship(s)

o In a committed relationship(s)

o Other:

7. How many people have you had sexual encounters with?

o 0

o 1 - 5

o 6 - 10

o 11 - 20

o 21 - 50

o 51+

o Prefer not to say

o Other:

8. How would you rate your own overall self-assessed attractiveness? (1 being extremely unattractive, to 10 being extremely attractive).

1 2 3 4 5 6 7 8 9 10

9. If you were seeking a casual relationship, please rank how important you find the following attributes in a potential partner. (1 being most important, to 5 being least important)

Attributes: Physical attractiveness, Well paid job, Good sense of humour, Intelligence, Kind & understanding

1.

2.

3.

4.

5.

10. If you were seeking a committed relationship, please rank how important you find the following attributes in a potential partner. (1 being most important, to 5 being least important)

Attributes: Physical attractiveness, Well paid job, Good sense of humour, Intelligence, Kind & understanding

1.

2.

3.

4.

5.

11. Do you think love needs sex?

o Yes

o No

o Sometimes

12. Do you think you can separate love and sex?

o Yes

o No

o Sometimes

13. Have you / do you think you could love more than one person simultaneously?

o Yes

o No

14. Have you ever had or thought of having a casual sexual encounter with someone?

o Yes

o No

15. Have you ever had or thought of having a casual sexual encounter with someone, whilst being in love with someone else?

o Yes

o No

o N/A

16. If you were in love with one person, have you ever felt sexually attracted to anyone else?

- Even if it was only someone you saw once?

o Yes

o No

o N/A

17. While in a relationship, would you have a casual sexual encounter with someone else?

- Even if someone you were incredibly attracted to proposed it?

o Yes - I would do it several times

o Yes - I would do it, but only once

o Yes - I would consider it, but wouldn't go through with it, despite wanting to

o No - I would never consider it, even if I felt I wanted to

o No - I would never consider it

18. Have you / would you have a relationship with someone who you knew was already in another relationship?

o Yes

o Yes - but for a casual relationship only

o Yes - but for a committed relationship only

o No

19. If you were to enter a relationship, would it make a difference if you knew they have children?

o Yes

o Yes - I would be put off for a casual relationship only

o Yes - I would be put off for a committed relationship only

o No

20. Do you think love should be separate from casual sexual encounters?

o Yes

o No

o Sometimes

Supplementary material S2. List of online resource platforms used to distribute questionnaire for data collection.

Facebook, Twitter, Reddit r/SampleSize community page (https://www.reddit.com/r/SampleSize/), personal website and blog (http://www.lillypharvey.co.uk/be-part-of-research/), University of Lincoln internal communications, Sex and Psychology website run by Dr. Justin J. Lehmiller, Harvard University (http://www.lehmiller.com/sex-studies/), and Psychological Research on the Net website run by Prof. John H. Krantz, Hanover College (http://psych.hanover.edu/Research/exponnet.html).

Supplementary material S3. Table summary of the number of responses per variable (with abbreviations) taken from finalised dataset of 713 participant responses.

Variable		Number of Responses	Response Percentage of Total Sample (%)
	19 – 24	431	60.7
	25 – 30	129	18.1
	31 – 40	91	12.8
	41 – 50	40	5.6
	51 – 60	14	2
	60 +	9	1.3
Gender	Female	454	63.7
	Male	269	36.3
Sexual orientation (sexor)	Heterosexual	562	78.8
	Homosexual	52	7.3
	Bisexual (Other)	99	13.9
Height (cm)	≤ 154	26	3.6
	155 – 164	211	29.6
	165 – 174	246	34.5
	175 – 184	160	22.4
	185 +	70	9.8
Self-assessed attractiveness ratings (selfatt)	1	3	0.4
	2	42	5.9
	3	90	12.6
	4	49	6.9

	5	55	7.7
	6	130	18.2
	7	187	26.2
	8	131	18.4
	9	18	2.5
	10	8	1.1
Sexual partners (sexenc)	0	69	9.7
	1 – 5	328	46
	6 – 10	121	17
	11 – 20	92	12.9
	21 – 50	72	10.1
	51 +	31	4.3
Casual sex whilst in relationship (rshpcas)	Yes	544	76.3
	No	169	23.7
Love more than one person simultaneously (lovetwo)	Yes	407	57.1
	No	306	42.9
Love needs sex (loveneedsex)	Yes	212	47.7
	No	163	29.7
	Sometimes	338	47.4
Separate love and sex (seplovesex)	Yes	625	87.7
	No	88	12.3
Casual sex (cassex)	Yes	608	85.3
	No	105	14.7
Casual sex whilst in love (lovecassex)	Yes	300	42.1
	No	357	50.1
	N/A	55	7.7
Sexually attracted to other whilst in love (lovesexatt)	Yes	104	14.6
	No	564	79.1
	N/A	45	6.3
Partner in other relationship (rshpother)	Yes	266	14.6
	No	447	79.1
Love separate from casual sex (lovesepcas)	Yes	333	46.7
	No	80	11.2
	Sometimes	300	42.1

Supplementary Material S4. Table summary of correlation outputs from Cramér's association coefficient test, identifying the strength of similarity between each combination of dependant variables within this dataset (*see Methods*). Refer to *Supplementary Material S3* for abbreviations.

Correlated Variables	**Cramér's Association Coefficient**

Lovetwo:Rshpcas	0.24
Lovetwo:Loveneedsex	0.06
Lovetwo:Seplovesex	0.07
Lovetwo:Cassex	0.14
Lovetwo:Lovesexatt	0.34
Lovetwo:Rshpother	0.28
Lovetwo:Lovesepcas	0.29
Rshpcas:Loveneedsex	0.04
Rshpcas:Seplovesex	0.07
Rshpcas:Cassex	0.25
Rshpcas:Lovecassex	0.35
Rshpcas:Lovesexatt	0.36
Rshpcas:Rshpother	0.24
Rshpcas:Lovesepcas	0.14
Loveneedsex:Seplovesex	0.18
Loveneedsex:Cassex	0.17
Loveneedsex:Lovecassex	0.09
Loveneedsex:Lovesexatt	0.06
Loveneedsex:Rshpother	0.07
Loveneedsex:Lovesepcas	0.08
Seplovesex:Cassex	0.04
Seplovesex:Lovecassex	0.10
Seplovesex:Lovesexatt	0.12
Seplovesex:Rshpother	0.08
Seplovesex:Lovesepcas	0.18
Cassex:Lovecassex	0.36
Cassex:Lovesexatt	0.22
Cassex:Rshpother	0.21
Cassex:Lovesepcas	0.10
Lovecassex:Lovesexatt	0.27
Lovecassex:Rshpother	0.23

Lovecassex:Lovesepcas	0.06
Lovesexatt:Rshpother	0.16
Lovesexatt:Lovesepcas	0.08
Rshpother:Lovesepcas	0.07